MADROÑO, Vol. 66, No. 4, pp. 148–163, 2019

BIOLOGY OF THE EPHEMERAL GEOPHYTE, STEER'S HEAD (*DICENTRA UNIFLORA*, PAPAVERACEAE) IN THE SOUTHERNMOST CASCADE RANGE, BUTTE COUNTY, CALIFORNIA

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ABSTRACT

Dicentra uniflora Kellogg (Papaveraceae), a small, single-flowered, ephemeral geophyte, was studied at three main and several secondary forest sites at the southern end of the Cascade Range in California (2009–2018). Emergence was closely linked to snowmelt, with flowering to senescence taking six to seven weeks, at elevations ranging from 1350–2575 m. Plants transitioned from flowering to fruit maturation within three weeks. Percent seed set in this perennial was high, ranging from 81–93% over five sites; seeds per fruit ranged from 44–83. In 2018, weekly field observations quantified the fate of flowers on plants staked when flowers appeared: only 27–43% of the flowers produced mature fruits with seeds, 23–24% dried up, and 25–30% disappeared, often leaving the pedicels. Black-tailed deer are suspected to be the primary herbivore, although nocturnal larvae of the butterfly *Parnassius clodius*, known to consume *Dicentra* leaves, may also be responsible at higher elevations. Each seed bears an easily-dislodged elaiosome, but little of the expected seed dispersal by ants was seen throughout the study. Field plantings of seeds illustrated that germination can occur in winter, below the snow, with seedlings bearing only a single cotyledon emerging from the ground in the spring. A seedling quickly produces a tiny food-storing, belowground bulblet before disappearing with the summer drought of the Mediterranean-type climate. The second-year plant produces a new bulblet and sometimes a tiny tuber, but only a single leaf, and plantings in the field suggest that it may take up to 10 years or more before an individual reaches flowering stage. A flowering plant has one or two fusiform tubers approximately 21 mm long and a cluster of ~9 whitish bulblets approximately 4 mm long. Published research in the closely-related *D. cucullaria* (L.) Bernh. indicates that bulblets are undeveloped food-storage leaf bases unique to four species of *Dicentra*, capable of giving rise to small plants and providing food for plant development. Bulblets planted in this field study clearly indicate they are capable of asexual reproduction. As in some other geophytes, dry weight of *D. uniflora* tubers was significantly greater in June at the beginning of the summer drought than in November when the plants began renewed root growth early in the fall wet season. The depth to the tops of tubers on plants occurring in clusters varied from 3.2–10.7 cm in the rocky, loamy or sandy-loamy soils of these sites.

Key Words: bulblet, *Dicentra uniflora*, elaiosome, geophyte, high seed set, *Parnassius clodius*, phenology, tuber.

When in flower, the steer's head, *Dicentra uniflora* Kellogg (Papaveraceae) (Fig. 1A) attracts photographers and plant collectors. Local floras often note that this species flowers soon after snowmelt, but the rest of the life cycle of this small plant is not well known. Literature on its ecology is very limited, even though this species has a wide geographic range, from southern British Columbia, south to the North Coast Ranges and the Sierra Nevada, CA, and east and south to the mountains of Montana, Wyoming and Utah (Stern 1997). This species was included as characteristic of a snowbed plant community in the western Cascades in Oregon (Hickman 1976).

This ephemeral perennial, about 3-7 cm tall, is the smallest of the 20 species in the genus *Dicentra* Bernh. (Stern 1997). One or two dissected leaves and a single flower appear annually, and the entire plant disappears aboveground, as it senesces in six to seven weeks. The term "geophyte" has apparently not been applied to this species, although its quick drying down to the tuber after the wet season, is consistent with that life form (Dafni et al. 1981; Rundel and Anderson 2016). Most reports on geophytes focus on monocotyledonous plants (e.g., Rundel 1996), not on dicotyledonous species such as *D. uniflora*. This species is acaulescent, and descriptions in floras often indicate the plants have a cluster of whitish bulblets at the top of the tubers (Stern 1997; Baldwin et al. 2012). A detailed morphogenesis study on four species of *Dicentra* by Walton and Hufford (1994) helps explain the complex belowground organs of this species and emphasizes the asexual role of the bulblets. The monograph of *Dicentra* (Stern 1961) provided extensive morphological and anatomical data and included a phylogeny for the genus.

Some ecological information was provided by Berg (1969) involving the elaiosomes and carriage of the seeds by ants. A recent report covered some features of habitat and reproductive biology for the *D. uniflora* in British Columbia (Courtney and

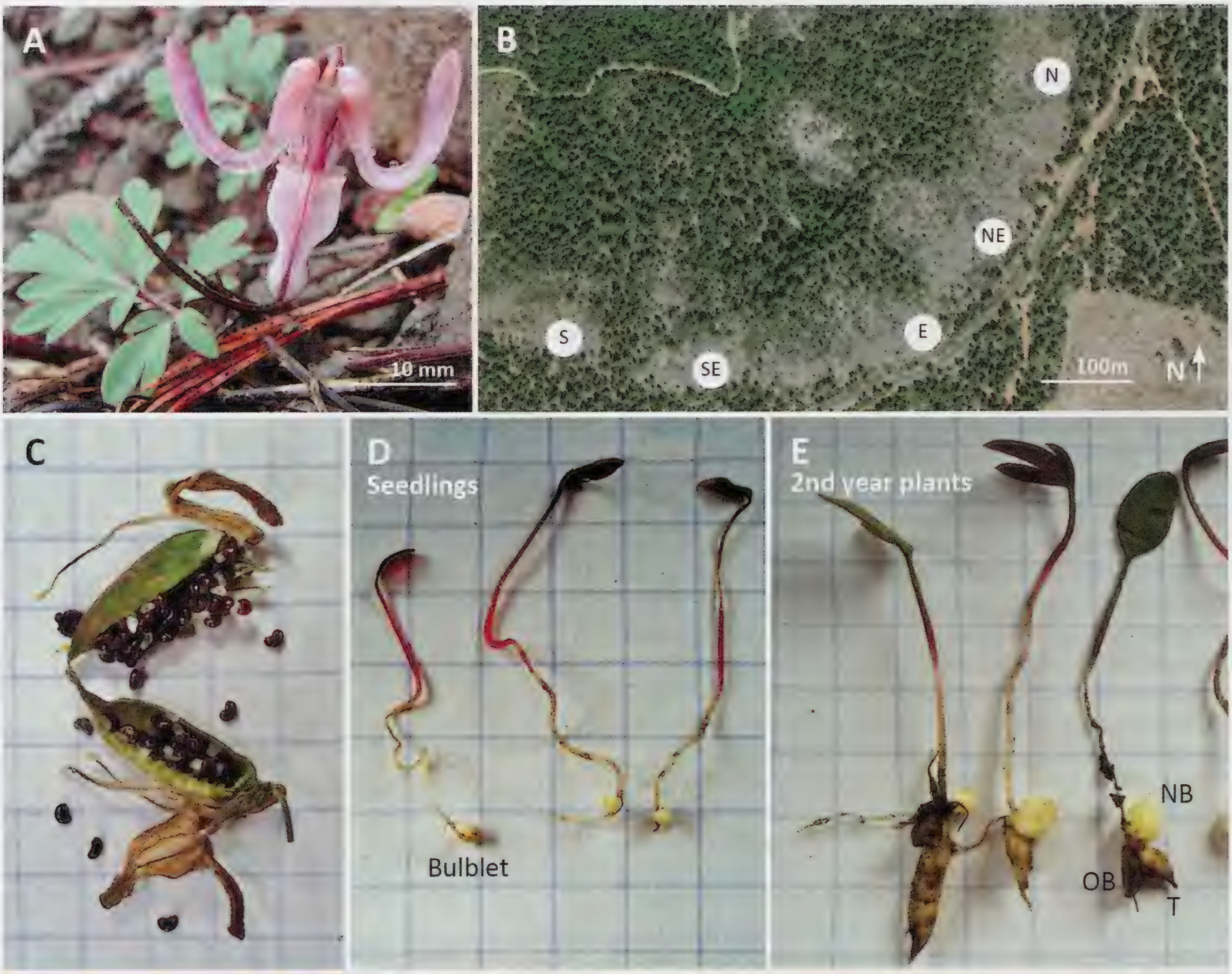

FIG. 1. Biology of *Dicentra uniflora*. A. Plant with single flower (photograph by Robert D. Fischer). B. Aerial view (from Google Earth) of the Tuscan Formation outcrop "crescent" on Carpenter Ridge, Butte County. The five study areas in open coniferous forest adjacent to the steep rock outcrop are indicated by letters N, NE, E, SE, and S. The USGS benchmark is located in study area E at 4535 ft (1383 m) elevation. C. One split-open fruit, showing several of the small, whitish elaiosomes visible against the black seeds (5 mm grid). D. Seedlings, with small bulblets on the underground portions (5 mm grid). E. Second-year plants, each with a brownish old (spent) bulblet (OB), a new cream-colored bulblet (NB), and a small tuber (T) (5 mm grid). F. Mature tubers, showing cluster of bulblets attached to the condensed stem axis at the top of two fresh tubers and two old, desiccated tubers. New roots were emerging on this plant when collected on 5 November 2010. G. Caterpillar of *Parnassius clodius*, a probable herbivore on *D. uniflora* leaves and fruits at the higher elevation study sites. Collected at the Summit study site. H. Adult butterfly, *Parnassius clodius*, also collected at the Summit study site. These distinctive butterflies indicate the larval stages are likely present as herbivores on *Dicentra* species in an area.

Scotter 2018), and the biology was briefly described for the species in Utah (Rayl 2002). In January 2019, at the 9th Symposium of the Northern California Botanists, the authors presented the first descriptions of the growth patterns observed from field plantings of seeds and bulblets, as well as survival of flowers and fruits at varied elevations ranging from 1350 to 1940 m. *Dicentra uniflora* is listed as one of the larval food plants for a species of butterfly, *Parnassius clodius* Ménétriés, Papilionidae (Scott 1986; Pyle 2002; Shapiro and Manolis 2007; James and Nunnallee 2011). Diane Debinski (Montana State University, personal communication) and her colleagues (e.g., Aukland et al. 2004) have focused on the plant as host to the butterfly larvae and its relation to climate change in Montana.

After this species was collected at Butte County sites in the southernmost Cascade Ranges of California in the spring of 2009 (Appendix 1), a search for published information indicated there was very little known about the biology of the plant. The purpose of this field study was to elucidate/describe features of the entire life cycle of *D. uniflora*. The major goal was to document its overall phenology by examining the plant in several sites at different elevations within a limited region over several years. Within this phenological context, several of the most important questions we wanted to answer were: 1) how similar are the times of emergence, reproduction and senescence in different years, 2) how successful are the plants at producing seeds, 3) when and where do seeds germinate, and 4) what is the timing and pattern of growth of the seedlings, bulblets, and tubers? This report presents results from the first part of our long-term field studies on *D. uniflora*.

MATERIALS AND METHODS

Study Sites

To incorporate potential variation from the plants in the southernmost Cascade Range, three main study sites in northeastern Butte County were used (Appendix1). Additional observations were made in another Butte County site (Humboldt Peak) and at Lassen Volcanic National Park (LVNP). Bedrock for all Butte County sites is Tuscan Formation volcanic mudflow. Soils in the three Butte County sites are rocky, and consist of sandy loam or loam, as determined with separate composite soil samples taken for each site in 2009 and sent to A. & L. Analytical Laboratories, Inc., Memphis, TN (Kannely and Schlising 2014).

All study sites have a Mediterranean-type climate, with a shorter winter-wet season at the lowest site than at the other sites. The lowest site (Carpenter Ridge) has a weather-recording station about 1.7 km distant, and at an elevation of 1735 m, or 350 m higher, from which climatic measurements were available for 2008–2018 (CA Department of Water Resources 2018a). Precipitation and temperature data from this source were used to approximate conditions for Ridge and the other main sites in Butte County. Another study site (Humbug Summit) had snowfall data available for 2008–2018 (CA Department of Water Resources 2018b). Snowfall and rainfall data for LVNP study site (Brokeoff Trail) were obtained for 2008–2011 (CA Department of Water Resources 2018c,d).

Three main study sites. The three main study sites, at different elevations, were visited frequently in spring and early summer during the entire, short aboveground cycle of this ephemeral geophyte. Secondary sites were visited less frequently to provide supplemental information.

Ridge.—The lowest main study site, Carpenter Ridge, or "Ridge," is about 6.9 km southwest of Butte Meadows, at 40° 03′ 19.9″ N, 121° 35′ 40.1″ W, and has a USGS benchmark at 1383 m elevation at its center. *Dicentra* plants were studied in five disjunct areas on or near the top of Ridge, differing in elevation by no more than 30 m. Main forest trees are *Pinus ponderosa* Lawson & C.Lawson, *P. lambertiana* Douglas, *Pseudotsuga menziesii* (Mirb.) Franco, *Calocedrus decurrens* (Torr.) Florin, *Abies concolor* (Gordon & Glend.) Lindl. ex Hildebr., and *Quercus kelloggii* Newb.; shrubs include *Ceanothus integerrimus* Hook. & Arn. and *Arctostaphylos patula* Greene (Kannely and Schlising 2014). Soils in all five areas are sandy loams, with percent particles ranging from 60.8 to 74.7 (sand), 17.2 to 29.4 (silt), and 5.4 to 9.7 (clay).

The five areas at Ridge extend over a length of about 805 m, and vary from each other in exposure and slope, and are named according to their position on the major "crescent" formed here by Carpenter Ridge (Fig. 1B). Ridge N is the area farthest north; it is unshaded and has the most southerly exposure (WNW). Few herbaceous plant associates were in flower with *Dicentra*, mainly *Sanicula tuberosa* Torr. and *Microsteris gracilis* (Douglas ex Hook.) Greene—two associates known at all five study areas here. Ridge NE, farther to the south, has some shade from trees and a sprinkling of pine needles on the ground. Flowering associates include *Allium campnulatum* S.Watson, as well as the *Sanicula* and *Microsteris*, and has an exposure to the NW. Ridge E (with the USGS benchmark) is unshaded, with the associates mentioned, as well as *Hemizonella minima* A.Gray, and has a NNW exposure. Ridge SE is shaded part of the day. Additional associates include *Castilleja applegatei* Fernald subsp. *pinetorum* (Fernald) T.I.Chuang and Heckard. It has an exposure to the north. Ridge S, the southwestern-most area, has only the upper part shaded and exposure is to the north. Flowering associates are mainly *Sanicula*, *Microsteris* and *Hemizonella*. The loamy soil here has the lowest percentage of clay particles (5.5%) and the highest percentage sand particles (74.7%) of the five areas studied and has sparse litter. The Mediterranean climate results in most precipitation falling from mid-October to mid-May. Snow melts first at Ridge N and last at Ridge S each spring.

Meadow.—The second main study site, "Meadow," is located 6.6 km east of Jonesville, and 0.3 km south of the road along Scotts John Creek, on U.S. Forest Service road 26N27, at 40° 06′ 21.0″ N, 121° 25′ 35.40″ W, and 1746 m elevation (Kannely and Schlising 2014). *Dicentra uniflora* grows mainly in a zone between dense forest trees and a wet meadow, and in an adjacent open, drier meadow. Some plants receive shade from trees during flowering, others are not shaded; aspect is to the northwest. Trees are mostly *Abies concolor* and *Pinus jeffreyi* Balf.; shrubs include *Symphoricarpos mollis* Nutt. and *Ribes roezlii* Regel. Early-flowering herbaceous associates are *Hackelia californica* (A.Gray) I.M.Johnst., *Allium campanulatum*, *Collinsia torreyi* A.Gray var. *wrightii* (S.Watson) I.M.Johnst., and *Dicentra pauciflora* S.Watson. *Dicentra formosa* (Haw.) Walp. is also common in the surrounding forest. Soil is a loam (50.8% sand, 35.4% silt, 13.7% clay); litter from trees occurs primarily on *Dicentra pauciflora* and *D. formosa* plants. This site, 360 m higher than Ridge, has snow persisting longer. In all years of the study, snow on the local unpaved roads prevented spring observations until late May or early June.

Summit.—The third main study site, "Summit," occurs on Humbug Summit Road, 1.5 km south of Humbug Summit, at 40° 6′ 20.6″ N, 121° 23′ 27.7″ W, and 1945 m elevation, 560 m higher than Ridge. *Dicentra uniflora* was studied on a small, open slope facing the southwest, in a forest of red fir (*Abies magnifica* A.Murray bis) and some *Pinus contorta* Douglas ex Loudon subsp. *murrayana* (Grev. & Balf.) Critchf., where the plants receive at least some shade daily during the reproductive season. Main associates flowering with *Dicentra* include *Hackelia nervosa* (Kellogg) M.Johnst., *Allium campanulatum*, and *Collinsia torreyi* var. *wrightii*. Soil is a sandy loam (60.8% sand, 29.4% silt, 9.6 % clay); there is more conifer litter on the soil than at the other two sites. The climate here is similar to that of the Meadow site, with an additional one to two weeks for final snowmelt in this shaded study site. This site was typically not accessible until early or mid-June.

Secondary study sites. Humboldt Summit.—Short segments of the Pacific Crest Trail in northern Butte County east and west of the Humboldt Summit Road were visited on 15 June 2009. Mature fruits from two populations of *D. uniflora* were located at 500 m west of the parking area at approximately 2050 m in elevation in semi-open areas with loose rocky soils (Janeway 2019).

Lassen Volcanic National Park.—Brokeoff Trail was surveyed several times during the spring and summer of 2009 and 2010. The trail begins near Highway 89 and ends at the summit at 2815 m. Populations of *D. uniflora* were observed at 15 locations beginning near the lower portion of the trail at 2065 m to the timber line at 2575 m. Mature fruits were collected in both years, from large populations along lower Brokeoff Trail 40° 25′ 46.73″ N, 121° 32′ 26.00″ W, at 2100 m, and along mid-Brokeoff Trail 40° 26′ 5.27″ N, 121° 32′ 49.78″ W, at 2240 m. The lower site is more forested and less open, and *Claytonia lanceolata* Pursh flowers occurred frequently with *Dicentra*. Hickman (1976) also noted that *C. lanceolata* was an associate of *D. uniflora* in Oregon.

Vegetation Transects

To understand the habitat where *D. uniflora* grows in the Butte County sites, transects were laid out in 2009 and 2010. Ten 1-m^2 plots were established one m apart along each of the 21-m transects at each of the main study sites. In each of the 1-m^2 plots the following were recorded: the number of single, bi-lobed, and tri-lobed leaves; the total number of leaves; the number of leaves in clusters; the numbers of flowers or fruits; and the soil depth within any clusters of *D. uniflora* plants. The 1-m^2 plots were then sub-divided into 0.25-m square sections and data were collected on soil depth in cm at the center of each, by pushing a soil thermometer until resistance in the soil (i.e., rock or bedrock) stopped it in the very shallow soils. Plots were surveyed on Carpenter Ridge as follows: in 2009 (at S on 17 May); in 2010 (at E on 3 May, at N on 13 May, and at SE and S on 22 May). Plots were surveyed at Meadow and Summit on 11 June 2009 and 8 July 2010. During each site visit air and soil temperature data were collected.

Phenology

Historical. Data were reviewed for *D. uniflora* for northern California from the online database of the Consortium of California Herbaria (accessed 2009) and specimens were examined at the Herbarium at California State University, Chico, CA (CHSC). The area of interest (representative of the southernmost Cascade Range) was bounded by latitude north (N) and longitude west (W) as follows: 41° 0′ 0″ N, 123° 0′ 0″ W; 41° 0′ 0″ N, 120° 45′ 0″ W; 39° 25′ 0″ N; 20° 45′ 0″ W; 39° 25′ 0″ N, 123° 0′ 0″ W. Records were found from 1899 to 1998. Elevations ranged from approximately 1200 to 3200 m. Only those records from herbarium sheets with mature pink flowers and that had a clearly identifiable location and elevation were used. Plots of collection date versus elevation were developed to estimate changes in flowering phenology. The most notable features observed were the mature pink flowers and well-developed leaves.

Present-day study sites (2009-2018). The phenology of *D. uniflora* was evaluated at sites in northern Butte County in 2009—2011, 2017, and 2018, and for LNVP in 2009 and 2010. Each site was visited at approximately weekly intervals in the early spring after snowmelt. Sites were systematically walked to record the occurrence of early emergent leaves, flower buds, changes in flower color, fruit development, and senescence. Flowers were marked weekly in 2018 at the Butte County sites to better understand the timing, development, and fate of flowers and fruits. Fruits were considered mature once they had become brown, firm and plump. Only mature fruits were collected for seed counts. Observations of any indications of herbivory, disappearance of flowers or fruit (i.e., free-standing pedicels), non-matured fruits, chewed fruits, and dehiscent fruits were recorded. Senescence of leaves was indicated by a change in color from green to yellow, and finally brown. Changes in weather events, such as late snows, were recorded. Sites were monitored for four to seven weeks at a given elevation. Lower elevation sites were available in April until mid-June. Higher elevation sites were surveyed in June or early July.

When possible, some plant traits were measured systematically every meter along transects. But in years when there were few plants available, as many plants as could be found throughout the entire sample area had to be used. Main features measured were those that characterized growth and could be easily measured or assessed in the field or laboratory.

Reproductive Success

In 2018, small wooden stakes (Bamboo Paddle Picks, 11.4 cm long, Tablecrafts Products Company, Gurnee, IL) were inserted in the soil about five cm upslope from plants with flowers at the three main study sites. To determine how long individual flowers last and the timing of fruit and seed production, stakes were numbered with the week they were used to indicate new (pink) flowers. Weekly changes of these individual flowers were recorded, as from pink to brown, and then to plump/mature fruits before the seeds were lost (Fig. 1C). Stakes were removed as mature fruits were collected individually into #1 coin envelopes (Swinton Avenue Trading, Boca Raton, FL) for study in the laboratory. "Reproductive success" was scored as 1) flower had produced seeds, 2) flower had dried without producing seeds, or 3) the flower or developing fruit was entirely missing by the time the plant senesced.

Features of ovules and seeds. In the laboratory, fruits were examined with dissecting microscopes to count mature seeds versus aborted ovules, to determine ovules per ovary, seeds per fruit, and percent seed set. Seeds were counted as mature if they were black or very dark brown. Weights of the mature seeds were determined in 2009 by weighing 10 batches, each of 25 black seeds with their elaiosomes from fruits collected at Ridge in May. Similarly, 10 batches, each of 25 black seeds with their elaiosomes removed, were weighed to determine separate mean seed and mean eliaosome weights. To determine features of seed germination and the nature of seedlings (e.g., presence of bulblets and tubers), bulk and individual seed plantings were done.

Seed germination—bulk plantings. Batches of 50 seeds each were planted in the five areas at Ridge (15 July 2009 and 4 November 2010), and at Meadow and Summit (2 July 2009), before the fall rains began. Seeds were from fruits collected at the three main sites including each of the five areas at Ridge. Flat spots 30 × 30 cm had the soil loosened to about five cm, had four shallow furrows made, and had four v-creased strips of non-inked newspaper 20 cm long tucked into them to permit finding the seeds later. The strips were lightly sprayed with water, and each had 50 seeds spread along it before 1-1.5 cm of loose soil was spread over the entire planting and covered with a square of 0.25 inch hardware cloth secured with wire loops at the corners. Similar methods had been successfully used to germinate a geophyte with similar-sized seeds at the Ridge site (Kannely and Schlising 2014). Also, measurements of single-leaved seedlings of *D. uniflora* ($n = 19$) averaged 2.8 cm from soil surface to the belowground bulblets (made at the Brokeoff study site), which indicated using these depths were a reasonable approach for our initial field germination studies. These plantings received only natural precipitation. Rows of seeds in their supporting newsprint were recovered at intervals and examined in the laboratory.

Seed germination—individual seed plantings. On 6 July 2009, three plantings of 100 seeds of *D. uniflora* were made on Carpenter Ridge at E, SE, and S. Individual seeds were planted approximately 2.5 cm deep in 10 parallel rows, spaced five cm apart and with five cm spacing between each row. A pair of wooden toothpicks marked the end of each row. All sites had slopes of less than 5% and were cleared of small stones and larger pieces of woody debris. Corners were marked with small stones and each plot was photographed. Seeds planted at these three sites were from fruits collected earlier in the spring of 2009. Seeds were also planted at Ridge NE and N later on 13 July 2009. On 10 August 2009, individual seed plantings were also done at Meadow and Summit in the same manner as for the Ridge sites.

Counts of germinated seeds were made at weekly periods in the spring and early summer of 2010. Locations of germinated seeds were easy to recognize from the locations of the toothpicks, the regular spacing of the plantings, and the small cotyledons (Fig.1D) observed when the seeds germinated. Similar individual plantings were done in 2010. Seedling lengths (including cotyledons), as well as underground parts (as shown in Figs. 1D through 1F) were measured with calipers (General 152 mm Dial, General Tools and Instruments, Secaucus, NJ).

Tubers and Associated Bulblets

To elucidate the nature of the underground parts, entire plants were sampled at Ridge twice in 2010. The first sample was made 12 June, at the end of the wet season, when tubers were expected to be at maximum size/weight because of recent photosynthesis by the leaves (Fig. 1F). Tubers were washed in the laboratory to remove soil, dried, and gently brushed to complete soil removal. Cleaned tubers were further prepared by shaving off the caudex (top area of attachment of other parts) before measuring maximum diameter and length to the nearest 0.1 mm with calipers. Fresh weight was determined on a standard Mettler balance. Tubers were dried in an herbarium plant-press drier at 43°C for three months before re-weighing to determine dry weight.

The second sample was made on 4 November, at the end of the dry season, of plants that had been staked at Ridge S on 12 June so they could be re-located. The ellipsoid bulblets (Fig.1F) at the tops of the tubers were counted, removed from the plants, and combined together in a Petri dish. The whole set of bulblets were spread in a line and every 5th bulblet was sampled and cleaned of soil. The maximum diameter and length of each bulblet were measured to the nearest 0.1 mm. Dry weight was determined after drying for 11 weeks. The tubers bearing these bulblets were treated as with the June sample of tubers: cleaned, shaved at the top, weighed, dried, and re-weighed.

Statistical Analyses

Number of mature seeds per fruit (averaged for several years at each site) were compared across the three main sites (including three areas of the areas at Ridge), using a one-way ANOVA, followed by Tukey post-hoc tests. Seed set at these sites over four years were compared using a two-way ANOVA. Tuber dry weights and also maximum diameters were compared between samples collected before and after the hot, dry summer season using Student's t-tests. Linear regression of elevation versus day of the year (DOY) were used to compare herbarium collections of *D. uniflora* to determine pattern in the flowering phenology of this species in the region of this study. Data were analyzed using RStudio Statistical Computing (RStudio, Inc., Boston, MA).

RESULTS

The principal years showed different patterns of rainfall and snowfall, which influenced the phenological schedule of *D. uniflora* at all sites. Weekly visits to the sites as soon as they became accessible indicated how tightly the first emergence of *D. uniflora* is linked to snowmelt. The first leaves and flower buds were almost always visible as soon as the snow cover was lost and usually even as patches of snow still remained in protected places. Snowfall and rainfall patterns are typical of the northern California Mediterranean-type climate and summarized in Table 1. Snowfall data are not available for Carpenter Ridge. Snow frequently persisted in scattered patches on Carpenter Ridge until early or mid-April. For example, on 28 April 2010, there was still 30 cm to almost 100 cm of snow from N to S areas across the crescent shape of the ridge (Fig.1B). In 2017 approximately 15 cm of snow covered the ridge, and after that snow melted, another snowfall of 30 cm blanketed the ridge. Meadow and Summit had deeper snow and were not accessible usually until late May or mid-June or later. However, Meadow and Summit still were snow-covered on 2 June 2010 and 25 June 2017. Portions of Brokeoff Trail were not accessible until mid-June and early July in 2010 because of the much heavier snowfall.

TABLE 1. ANNUAL PRECIPITATION TOTALS IN CENTIMETERS FOR WATER YEARS (OCTOBER 1 THROUGH SEPTEMBER 30) FOR THE PRIMARY STUDY AREAS IN BUTTE COUNTY AND LASSEN VOLCANIC NATIONAL PARK (LVNP). Years are listed for when mature fruits and seeds were collected. See text for locations of weather stations, website addresses to data, and dates of access. NA = not available, NS = not surveyed.

	Snowfall (cm)		Total rainfall (cm)	
Water year	Summit	LVNP	Carpenter Ridge	LVNP
2008–2009	125	NA	119	127
2009–2010	149	253	135	147
2010–2011	208	NS	145	NS
2016–2017	254	NS	279	NS
2017–2018	119	NS	119	NS

The average daily air temperatures from the weather station near Carpenter Ridge demonstrate that Ridge was slightly cooler in the spring of 2010 than in both 2009 and 2018 (Table 2), the three years for which major phenology is presented in this paper. Average daily air temperatures for the LVNP Weather Station for 2009 and 2010 followed a similar pattern (Table 2). Air and soil temperature data taken at Ridge areas during the periods of fruit development were in the range of 15-20°C. Mid-summer air temperatures at Ridge seed and bulblet

TABLE 2. AVERAGE MONTHLY AIR TEMPERATURE IN DEGREES CELSIUS FOR SELECTED MONTHS FOR THE PRIMARY STUDY SITES IN BUTTE COUNTY AND LASSEN VOLCANIC NATIONAL PARK. Years are listed for when mature fruits and seeds were collected. See text for locations of weather stations, web site addresses, and dates of access. NS = not surveyed

Year	Month	Carpenter Ridge	Lassen Volcanic National Park
2009	April	7.7	5.4
	May	15.4	12.0
	June	16.3	13.4
2010	April	5.1	2.9
	May	8.2	5.9
	June	19.4	13.9
2011	April	5.6	NS
	May	8.2	NS
	June	14.7	NS
2018	April	8.7	NS
	May	13.9	NS
	June	19.8	NS

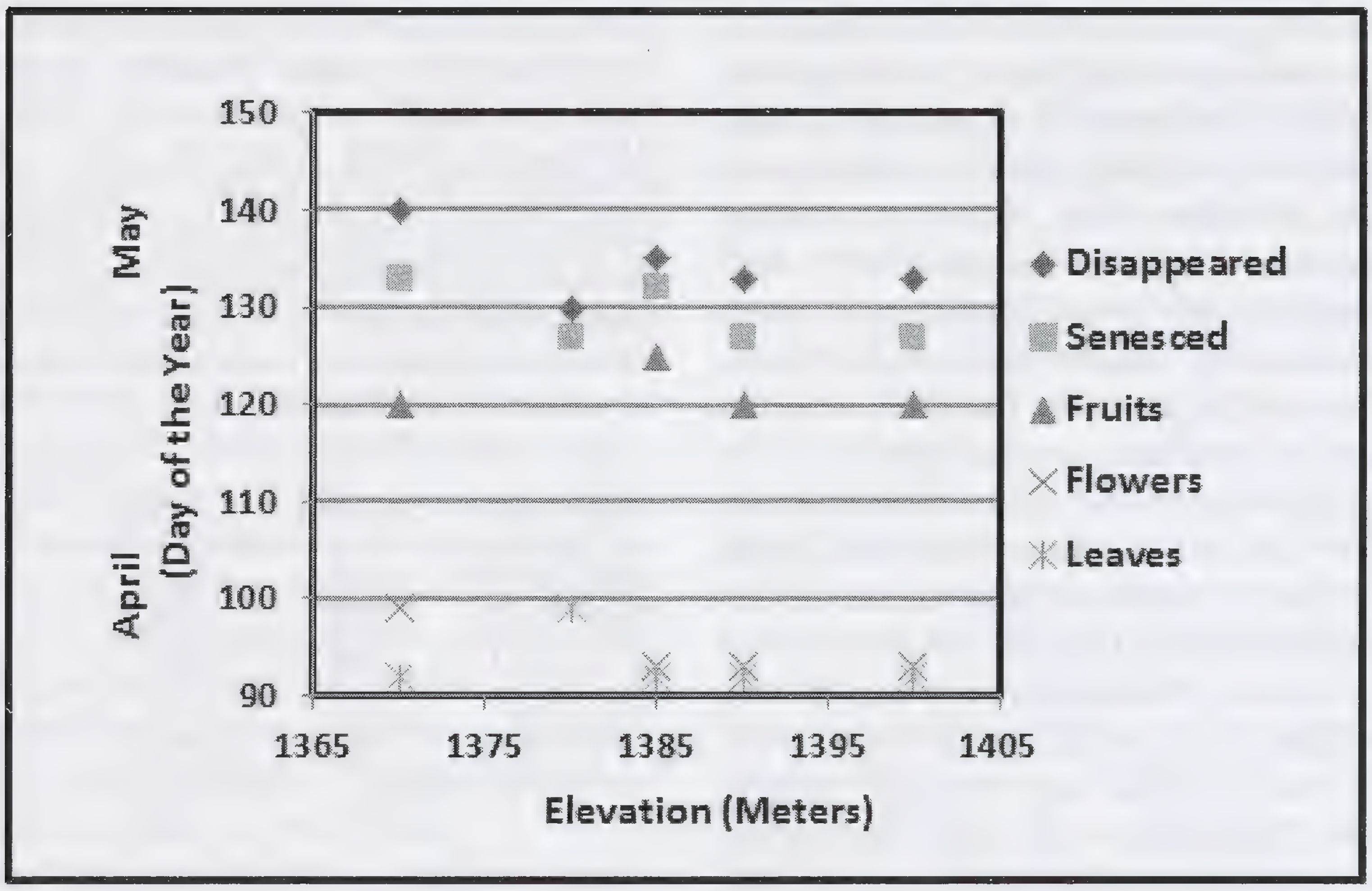

FIG. 2. Detailed phenology of *Dicentra uniflora* at the five areas of Carpenter Ridge in 2018, as representative of the typical phenology for this species. The timing of the first appearance of leaves and flowers occurred as shown by day of the year in early April 2018. Leaves and flowers appeared soon after snowmelt at the five study areas. Mature fruit development occurred in two to three weeks after first leaf and flower emergence. Senescence and disappearance of plants followed in another two to three weeks. The five columns of data points represent the phenological changes at the areas on Ridge from left to right, as follows: S, N, NE, SE and E.

planting sites were in the 30°C range; whereas mid-day soil temperatures at seed and planting sites commonly reached 40°C, or 10 degrees higher on the average, than air temperatures. These soil temperatures were almost as high as the temperature (43°C) used to dry the tubers and bulblets for evaluation of dry versus fresh weights. Mid-day air temperatures at Meadow and Summit seed and bulblet planting sites were 8 to 20 degrees less than Ridge due to the more shaded sites and were typically in the 20-23°C range. Soil temperature data taken at the Butte County sites beneath snow were in the 0.5 to 1°C range.

Plant Density

Percent cover is typically low for *Dicentra uniflora*–less than 1.5% (Jackson and Bliss 1982; Auckland et al. 2004). Cover was low at our study sites also. Number of leaves of all types from single leaves to clusters of highly dissected leaves ranged from a lowest mean of 0.025 ± SE 0.0025 per 1-m^2 at Ridge N (2009) to a highest mean of 11.325 ± SE 2.238 per 1-m^2 at Ridge S (in 2010) with single leaves being the most common. Low flower densities are also common, ranging from zero per 1-m^2 at Ridge N (2009) to 5.2 ± 1.590 per 1-m^2 at Ridge S (2010), making detection unlikely unless one visits a location soon after snowmelt and is looking specifically for this species.

Phenology

Recent. The development of *D. uniflora* from after snowmelt to senescence and disappearance usually takes six to seven weeks. Flowers change color very rapidly, usually within a week, and fruit development typically follows within another one and a half to two weeks. As the fruit develops, the flowers turn greenish and become brown, plump and firm. Fruits also become heavy and lie prostrate on the ground, and once mature, expose their seeds. Herbivory on fruits appears to occur during the maturing phase. Plant senescence typically occurs within two to three weeks after fruits mature and is noted by yellowing of the leaves, followed by browning, and shortly thereafter total withering and disappearance. Herbivory was never observed on green or yellowing leaves in this study. The typical phenological pattern is shown in Fig. 2 for Ridge areas. This general pattern may take a slightly shorter time period at higher elevations of perhaps a week (Fig. 3). The spring temperatures and snowmelt were similar in 2009 and 2018, and therefore fruits matured at about the same times in those two years in Butte County sites. Emergence of *D. uniflora* was about a month later at the locations for Ridge, Meadow, and Summit between 2009 and 2010. This pattern is similar to that observed on Brokeoff Trail in LVNP also (Fig. 4).

Historical. Herbaria collections from 1903—1998 show flowering dates from approximately 100 to 210 (as DOY) for elevations ranging from about 1200 to 3200 m (Fig. 5). As elevation increased, *Dicentra* flowered later in the year ($R^2 = 0.469$, df = 90, P <0.001, $y = 76.9 + 0.04x$). In other words, for each 100 m increase in elevation, there was a 4-day delay in flowering. This trend is consistent across similar elevations used in our studies in northern California (Fig. 5).

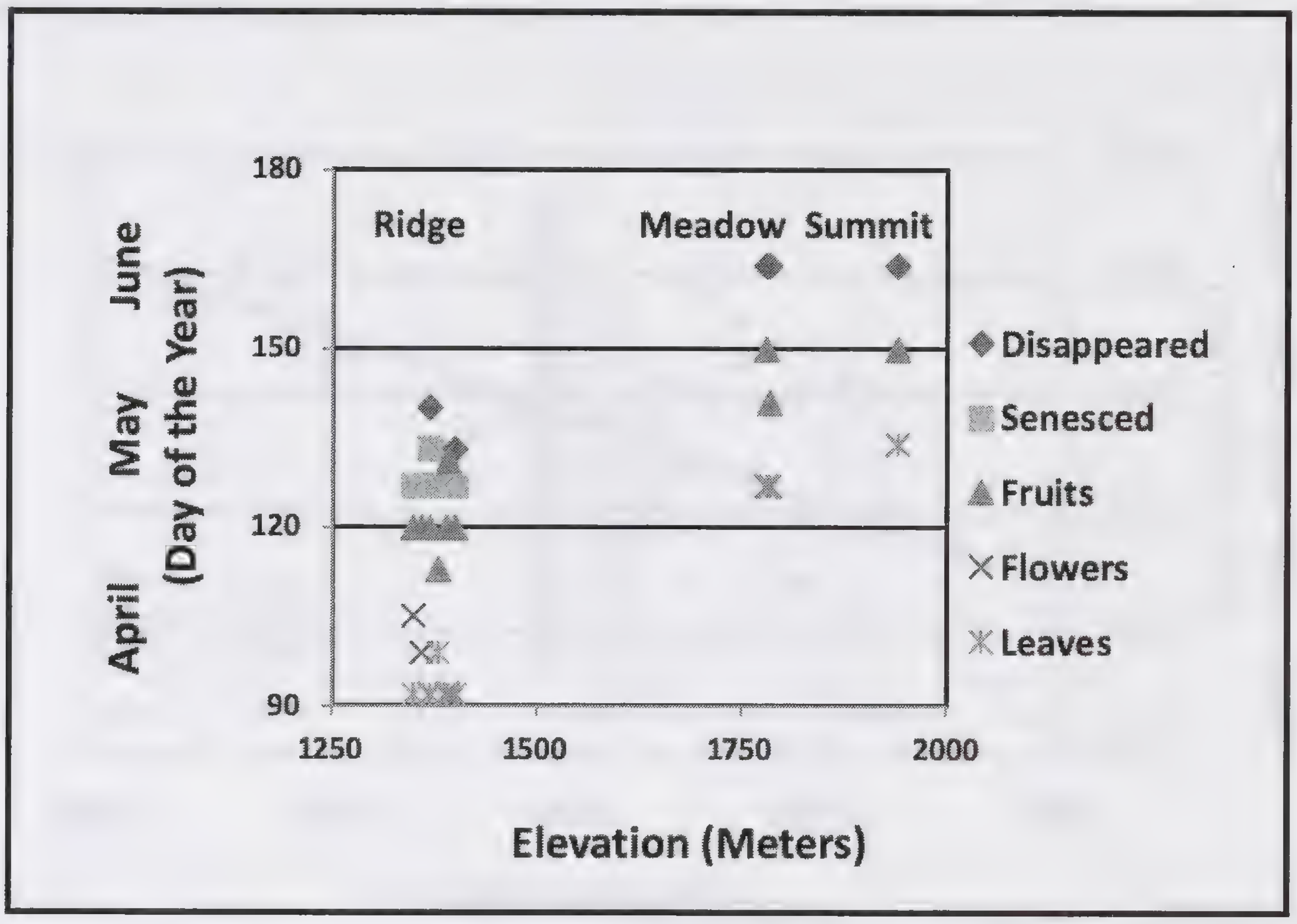

FIG. 3. Variation in phenology of *Dicentra uniflora* at the three main Butte County study sites (Ridge, Meadow, and Summit) for 2018. The timing and appearance of the first leaves and flowers soon after snowmelt is shown as day of the year. Leaves and fruits appeared in early April at Ridge (which included five study areas), and in early to mid-May at Meadow and Summit. Mature fruits appeared two to three weeks later. Senescence and disappearance of plants followed in another two to three weeks. The plants and fruits developed slightly faster at the higher elevation Meadow and Summit sites than at the lower elevation Ridge site, by perhaps one to two weeks. Symbols represent day of year for individual observations.

Reproduction and Growth

Fate of flowers in 2018. The fate of flowers on *Dicentra* plants staked in the spring of 2018 is shown in Fig. 6 and summarized across the three main sites as follows: 27-43% of the flowers produced mature fruits with seeds, 23-24% dried up, and 25-30% disappeared, often leaving the pedicels.

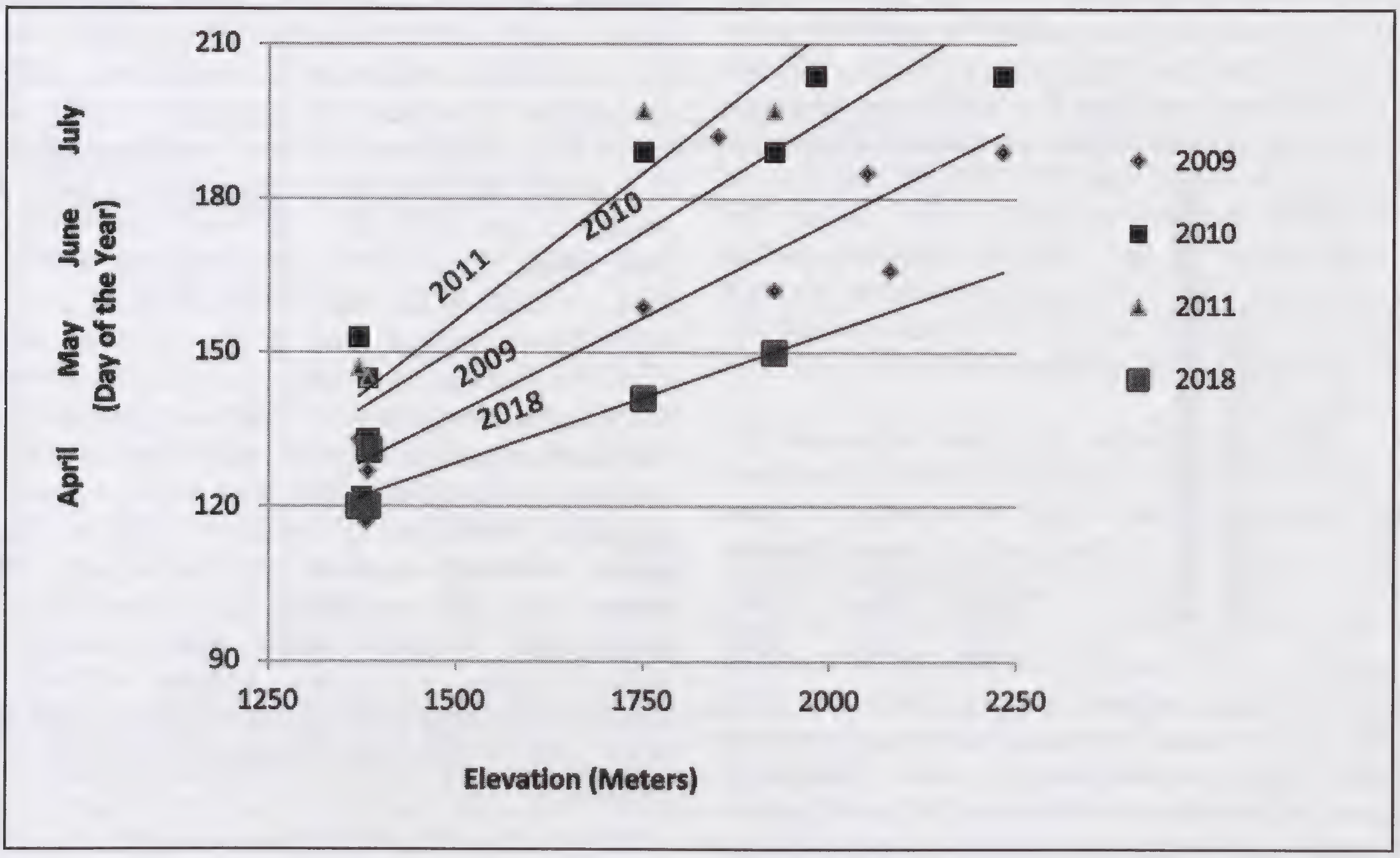

FIG. 4. Trends of mature fruit collections of *Dicentra uniflora* in 2009, 2010, 2011 and 2018 at study sites in Northern California showing influences of both elevation and weather patterns. Mature fruits were collected at Butte County and also at Lassen Volcanic National Park study sites in 2009 and 2010, but only at the Butte County sites in 2011 and 2018. The spring temperatures and snowmelt were similar in 2009 and 2018; therefore, fruits matured at about the same times in the Butte County sites in those two years. There was a cooler spring and later snowmelt in both 2010 and 2011 than in both 2009 and 2018; thus, fruits of *D. uniflora* matured later in 2009 and 2018.

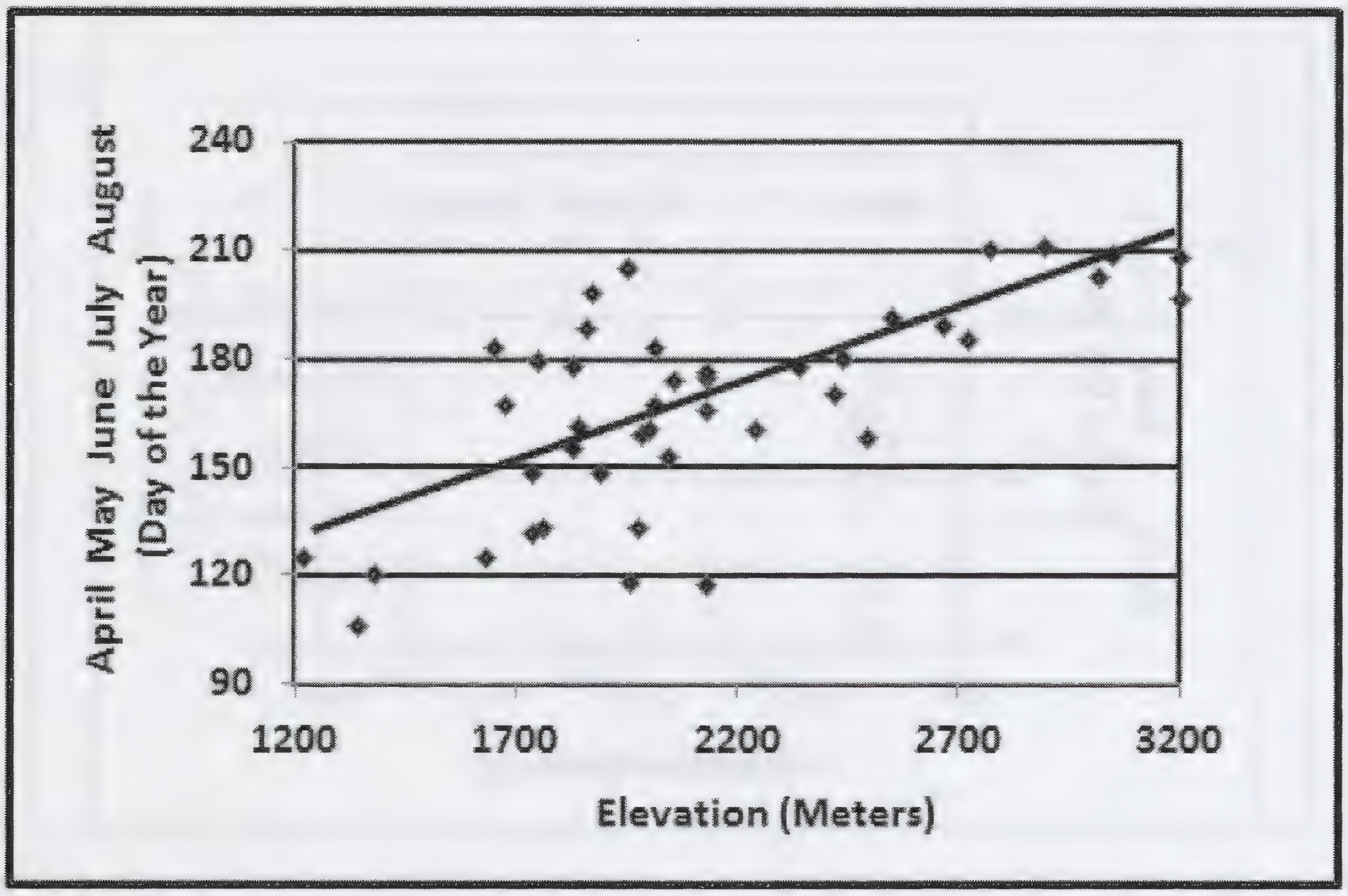

FIG. 5. Historical phenology of *Dicentra uniflora* in Northern California as indicated by collections of flowering herbarium specimens from 1903 through 1998. This linear regression shows the approximate day of the year of collection versus elevation from April through early August for 1903-1998. These collections were from 1250—3200 m in elevation, with higher elevation collections into early August.

Seeds per fruit. The number of mature seeds per fruit at the three main Butte County study sites varied somewhat in the four years that larger samples (n = 13 - 32) were obtained (Fig. 7A). These results show that the two higher elevation sites (Summit and Meadow) averaged more seeds per fruit than the lowest site, Ridge (ANOVA, F = 17.34, P <0.0001, df = 4). For example, on average Summit had more seeds per fruit than the three areas at Ridge, NE, SE and S (Tukey Post-hoc Test, P <0.009) and Meadow had more seeds per fruit than two areas at Ridge, SE and S (Tukey Post-hoc Test, P = 0.0028). Seeds from fruits listed for Ridge S in 2018 in Fig. 7A are the same fruits listed in the fate of recovered staked flowers shown in Fig. 6. The average number of seeds per fruit in *D. uniflora* in the 227 fruits counted for the four years at the three sites listed in Fig.7A was 62.8 ± SE 3.35.

Four additional samples at higher elevations (at the secondary study sites) had the following numbers of seeds per fruit (mean ± SE): Humboldt, 15 June 2009, 80 ± 6.6 (n = 32); Brokeoff, 30 June 2009, 64 ± 3.6 (n = 32); Brokeoff, 8 July 2009, 61 ± 4.2. (n = 22), and 23 July 2010, 67 ± 4.1(n = 25). Average seeds per fruit of *D. uniflora* for this entire study in the southernmost Cascade Range, combining data from the three main sites and the two secondary study sites listed here was 65.6 ± 2.6 (n = 325 fruits), in contrast to a mature seed count of 58 (n = 1) given by Courtney and Scotter (2018) and a reported seed count "greater than 50" per fruit (n = 82) by Rayl (2002).

Percent seed set. At all sites, counts of ovules that did not mature permitted determination of percent seed set. The mean number of ovules (developed and undeveloped) found in mature fruits listed for the three main study sites (Fig. 7B) was 70.4 ± SE 3.3. These ovules in mature fruits ranged from minute (possibly unpollinated) to partially developed, but wrinkled, and/or white–in sharp contrast with the black mature seeds. High percent seed set, ranging from 81–95%, occurred in the main sites of this study (grand mean of 87.6% in Fig. 7B), but with the two-way ANOVA indicating a significant difference among the three main locations (F = 11.41, df = 4, P <0.001). High percent seed set also occurred in Humboldt and Brokeoff sites (mean ± SE): Humboldt, 15 June 2009, 82 ± 3.7 (n = 19); Brokeoff 30 June 2009, 92 ± 2.1 (n = 32); Brokeoff, 8 July 2009, 84.5, ± 3.5 (n = 22) and 23 July 2010, 87.8 ± 1.9 (n =25). Mean percent seed set for all study sites was 87.4. No damage to ovules or seeds was observed in the 325 fruits examined to determine percent seed set, although occasional thrips were seen in the fruits, and occasional aphids were seen on the outside walls of fruits. Herbivory of seeds or fruits is described below. Although seed set per fruit is high, 80% or higher (Fig. 7B), we believe this occurs due to self-pollination. We have never observed any flower visitors during our many seasons of field visits. Stamens are appressed to the stigmas in the flower. Rayl (2002) had seed production in her bagged flowers.

Mature Seeds and Elaiosomes

Two hundred fifty shiny, black mature seeds from Ridge, weighed immediately after removing from fruits in May 2009, had an average weight per seed bearing an elaiosome of 0.5488 ± SE 0.0139 mg (Fig.

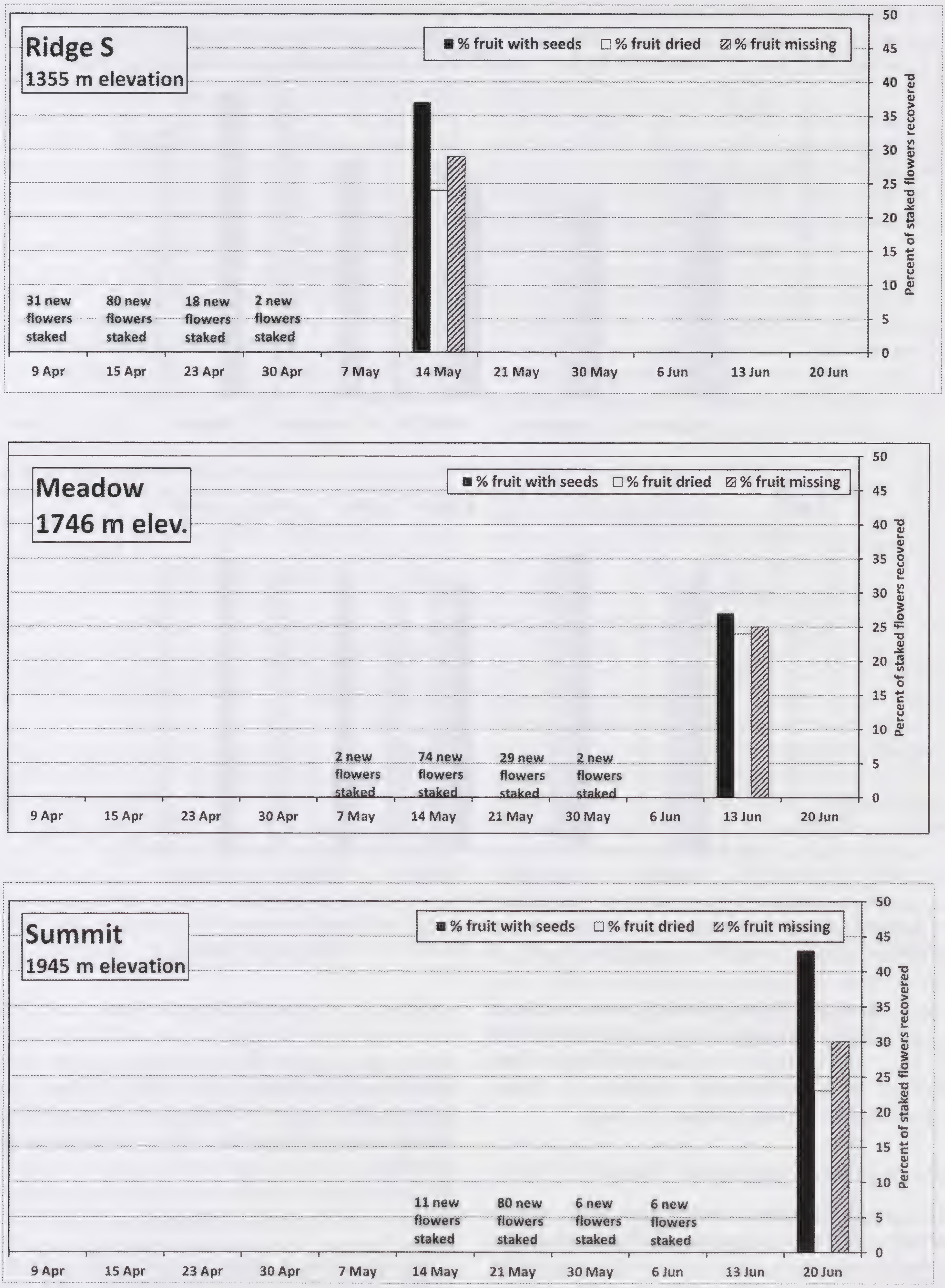

FIG. 6. Fate of staked *Dicentra* flowers at the three main study sites in Butte County in 2018. Each panel represents results at one of the three sites, showing dates flowers were staked (over a four-week period at each site) and dates when the fruits were recovered and assessed at each site. The three panels all have the same dates in 2018 listed across the horizontal axis to show how plants at the lower-elevation site (Ridge S—top panel) flowered and fruited earlier than at the other two, higher-elevation sites (Meadow and Summit). Fruits recovered at time of fruit maturation and plant senescence, were scored as percent of total flowers marked; percentages do not total 100% at a site because some stakes could not be relocated. Percent fruits with seeds = mature seeds present; % fruit dried = remains of ovary or young fruit present, but not producing seeds; % fruit missing = fruit gone, with or without pedicel still present.

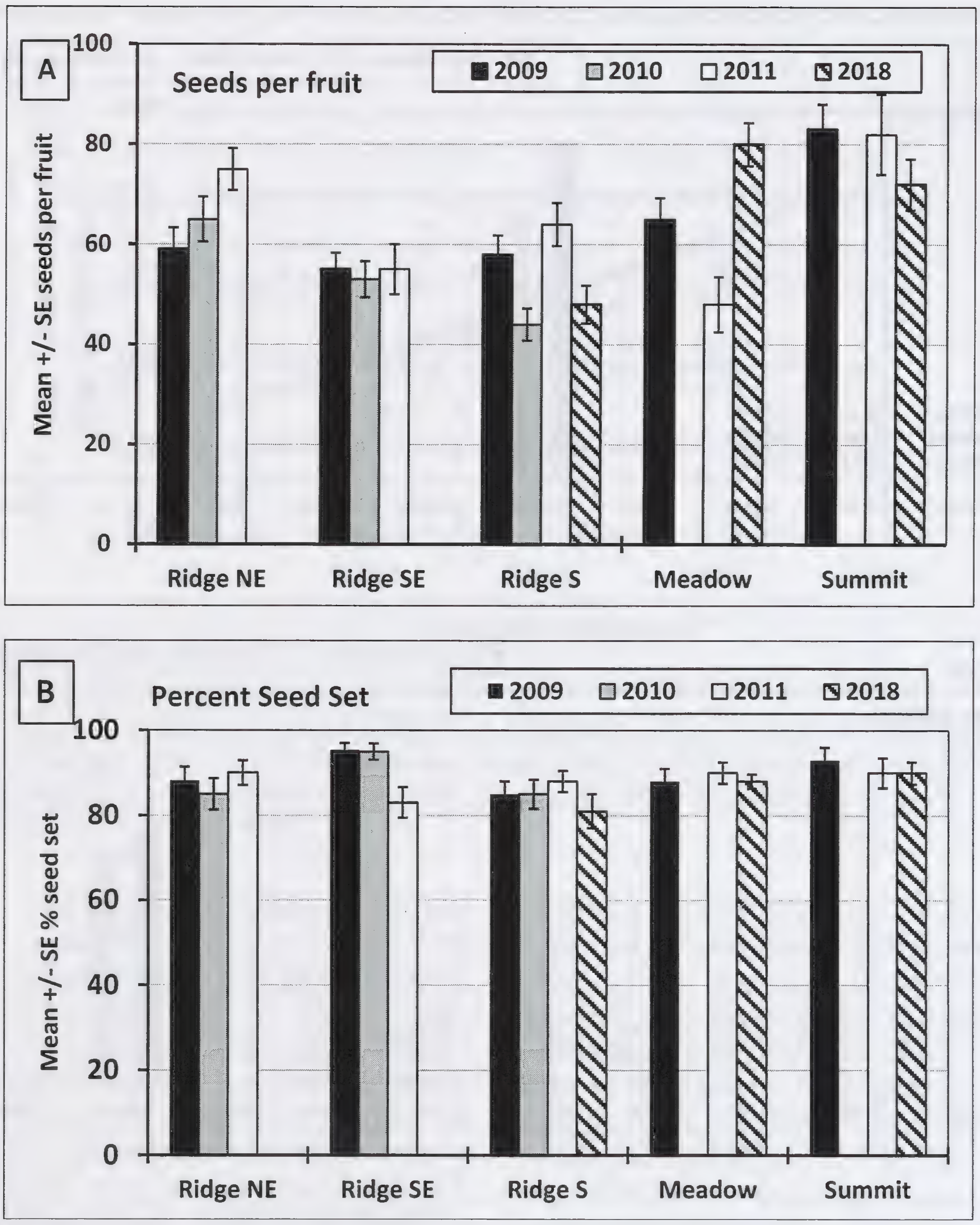

FIG. 7. Reproductive success in *Dicentra unilfora* at five study areas, over four years (n = 13 at Meadow, 2011; n = 18 - 32 in other years and areas). A. Mean ± SE seeds per fruit. B. Mean ± SE % seed set (n same as in Fig. 7A).

1C). Two hundred fifty additional seeds without elaiosomes had an average weight of 0.4994 ± SE 0.0178 mg. Thus, fresh elaiosome weight was estimated to be approximately 0.0494 mg. Elaiosomes detached very readily from the seeds.

Herbivory on Reproductive and Vegetative Parts

Each year, at all Butte County study sites, tracks of mule deer, *Odocoileus hemionus* Rafinesque, or the deer themselves were seen, but were not seen specifically browsing on *Dicentra* plants. Tunneling by Botta's pocket gopher, *Thomomys bottae* (Eydoux and Gervais), was common in the Meadow and Summit (but not Ridge) sites, but no specific destruction of *Dicentra* plants was noted. Bulblets of *D. uniflora* might be dispersed in the soil during tunneling by gophers, resulting in asexual reproduction (e.g., at Meadow and at Summit). A few examples of ants in fruits, or even carrying *Dicentra* seeds, have been recorded (at Summit, 16 July 2011 and 6 July 2018), but the ants were not collected or identified to species. At Summit, on 8 June 2018, a 16 mm-long black caterpillar or larva (Fig. 1G) was found on a partially eaten fruit. Also, an adult butterfly of *Parnassius clodius* (Fig. 1H) was captured nearby. Both were identified by Don Miller, California State University, Chico (personal communication).

Seed Plantings

Heavy erosion impacted the bulk plantings of seeds in the winters of 2009-10 and 2010-11. Remaining strips of paper bearing seeds and seedlings in soil were extracted with care, but seedlings were very small and delicate (Fig.1D), and some may have been missed during examination of the strips with dissecting microscopes. Plantings of individual seeds provided additional observations of the early germination features of *D. uniflora*.

Germination of at least some of the bulk-planted seeds occurred during the winter under snow. At Ridge N two strips of seeds planted on 15 July 2009 were dug on 17 December 2009. Black, hard seeds were found, with no signs of germination. But the next year, winter germination was confirmed with seeds planted in 2010, when strips bearing two and five germinated seeds were found at Ridge N on 4 February 2011. Cotyledons of seedlings appeared aboveground in all five different study areas at Ridge in April and May of 2010 and 2011. Each seedling had a single un-lobed cotyledon (Fig. 1D), sometimes with the seed coat still attached at the tip. Seedlings appeared later in the year at the higher elevation sites, visible at the soil surface soon after the snow melted, on 8 July 2010, with 29 cotyledons per paper strip at Meadow and 11 at Summit.

Many seedlings, apparently after photosynthesizing for a just few days (or possibly longer under the snow) had produced a bulblet (Fig. 1D). The largest sample of intact seedlings, collected when they were just reaching the soil surface (Ridge E and Ridge SE combined, on 12 May 2011, n = 36), had the following features (mean ± SE): length from tip of cotyledon to tip of root, 32.4 ± 1.83 mm (range 11-55 mm); maximum diameter of bulblet (n = 4) 1.0 ± 0.11 mm (range 0.7-1.2 mm).

A sample of seedlings about 3 weeks older that year (on 2 June 2010 at Ridge N) were somewhat larger: length from tip of cotyledon to tip of root (n = 8), 34.8 ± 1.9 mm (range 29.7-43.7 mm); maximum diameter of bulblets (n = 7) 1.43 ± 0.1 mm. Cotyledon blade (n =13) width was 1.9 ± 0.1 mm and length was 4.2 ± 0.2 mm. Measurements of seedlings from individual seed plantings in grid patterns compared well with the measurements presented here from bulk seed plantings. Seedlings at the three main sites (at different elevations) dried up above ground a few weeks after emergence, at which time the leaves of the adult plants were also becoming yellow or brown at senescence.

Below Ground Parts

Tubers. Representative below ground parts of a *Dicentra uniflora* plant are shown in Fig. 1F. Two new, pale tubers produced by the end of the spring growing season are shown in front of parts of two dark, withered tubers from the previous year that had produced the leaves and flowers in 2010. Fig. 1F also shows that fine roots had emerged from among the bulblets on the stem axis near the tops of tubers by early November. Average number of new tubers per plant was 1.6 ± 0.2 (n= 26). The depth to the tops of tubers on plants occurring in clusters ranged from 3.2 to 10.7 cm in the rocky, loamy or sandy-loamy soils of the sites.

Fresh weights (mean ± SE in g) were determined for new tubers collected at Ridge at two times in 2010. On 12 June fresh weights (0.366 ± 0.035, n =25) were higher than fresh weights (0.161 ± 0.027, n = 26) collected on 4 November. The June sample consisted of plants dug at the end of the photosynthesizing/flowering season. The November sample comprised plants that had persisted through the hot, dry summer season in the soil, but had received 20 mm rain by 8 September and 204 mm total rainfall just before being sampled.

Dry weights of the tubers collected on 12 June (0.188 ± 0.018) were significantly higher (Student's t-test, t = 2.54; P <0.05) than the dry weights of tubers collected on 12 November (0.118 ± 0.017). Grams dry weight lost over the summer were 36.98% of the dry weight of the June plants.

The mean maximum diameter (in mm) of new tubers, did not differ between the two samples (Student's t-test, t = -0.748, P = 0.458; June, 5.8 ± 0.2 versus November, 5.4 ± 0.25). Average length of tubers on flowering plants was 21.0 ± SE 2.5 mm. Average number of tubers per plant was 1.6 ± 0.2, determined from the November sample.

Bulblets. Plants collected on 4 November 2010 had (mean ± SE) 8.7 ± 1.0 whitish, ellipsoidal bulblets per plant clustered on the condensed stem axis to which tubers were also attached (Fig. 1F). Mean trait values of the bulblets (n = 31) were: length 4.0 ± 1.2 mm, maximum diameter 1.8 ± 0.1+ mm, fresh weight of 7.0 ± 0.3 mg, and dry weight of 6.6 ± 0.3 mg. It is not known if bulblet size (e.g., a range in length of 2.6 mm to 5.6 mm) relates to an increase in succeeding years, or if bulblets of different sizes on a plant were all produced in the same year and grew to different sizes. Bulblets were white and mealy throughout, with no obvious sign of an embryonic plantlet under a dissecting scope, although a very minute apparent bud meristem was visible at the base of the bulblet, similar to that reported by Walton and Hufford (1994) for *D. cucullaria*. All flowering *D. uniflora* plants sampled had bulblets, and most seedlings produced a single bulblet at the base of the petiole of the cotyledon (Fig. 1D). Bulblets planted in 2009 and 2010 produced small plants, each with a whitish (new) bulblet, and discolored remains of the old bulblet, and a small tuber.

DISCUSSION

Phenology

Our studies provide the first detailed quantitative information on the emergence of leaves and flowers of *D. uniflora*. The ephemeral nature of *D. uniflora* and the variation in weather phenomena from year to year require multiple years to understand the life history of this species. For example, in early June 2017, approximately 15 cm of snow-covered Ridge and numerous *D. uniflora* flowers emerged shortly after snowmelt and were marked with wooden stakes. Within a week, another snowfall of 30 cm blanketed the site, and nearly every marked flower and many new emergent leaves were frozen and lost for 2017. Meadow and Summit were visited in late June 2017, and numerous flowers were marked at both locations. Over the next two weeks these sites were visited and nearly all flowers/fruits were missing, probably due to herbivory. Thus, 2017, which started as an apparently "good flower and fruit spring," was essentially lost as a study year, with little phenological data collected at any site. The spring of 2018, by contrast, was a very good year for growth and seed production in *D. uniflora*, and we were able to collect excellent data at all three main study sites in northern Butte County.

Previous authors have noted the emergence of *D. uniflora* soon after snowmelt in northern California and the mountains of the western United States and Canada (Stern 1961; Hickman 1976; Jackson and Bliss 1982; Jackson 1985; Rayl 2002; Auckland et al. 2004; Courtney and Scotter, 2018), but there is no information on the time required from first appearance until fruiting and senescence. There is general information available on earlier emergence and flowering at lower elevations near 1200 m in British Columbia (Courtney and Scotter 2018) or high as 3280 m in the Slate Creek Valley in the Sierra Nevada of California (Jackson and Bliss 1982). In California herbarium collections, a flowering date as early as 28 March 1988 at 1209 m and as late as 11 July 1911 at 2895 m have been recorded. The range of elevations for the primary sites of this study, from a low of 1370 m for Ridge to 1945 m for Summit, thus fall in the mid-range of elevations for this species. Higher elevations from 2000 to 2600 m are included in two of the earlier years of our study (2009, 2010); thus, findings from this study have general applications to this species throughout its geographic range. The range of elevations from 1370 m (Ridge) to 1945 m (Summit) provide a four to seven-week period of snowmelt from the lower elevation to higher elevation; thus, as lower populations were maturing to fruit development, higher populations were just beginning to emerge. In 2018, it was even possible to mark the edge of the snowfield at Meadow and Summit study sites and record the emergence of flowers as the snowline receded. Figs. 3 and 4 illustrate the phenological patterns observed with snowmelt in our region in northern California for four years. Similar patterns of phenology are to be expected through the years throughout the range of *D. uniflora*.

Herbarium collections have focused on the flowering dates of this plant and its unique appearance. Leaves can resemble other plants and without the flowers, it can be easily overlooked (Courtney and Scotter 2018). The flowers mature to fruit rapidly in only two to three weeks, turning from green to brown. They tend to be prostrate on the ground (Berg 1969) as they become mature, begin dehiscing, and shrinking, making them even more difficult to observe. Given the low density of the flowers, marking flowers with small numbered wooden bamboo stakes was essential for tracking flowers and fruits and evaluating their fate (Fig. 6).

Seeds, Germination, and Seedlings

Nature of seeds and their elaiosomes. Growth and maturation of *Dicentra uniflora* seeds were described by Berg (1969). He illustrated that the elaiosome was of epidermal origin on the developing ovule, and that at seed maturity an elaiosome consists of only between six and eleven giant cells that "contain great quantities of fatty oils" (as determined by tests using Sudan IV). Berg noted that an elaiosome breaks loose from a seed very easily, and that this may be why Stern (1961) described *D. uniflora* seeds as lacking elaiosomes in his systematic treatment of the genus. Fukuhara (1999) presented an electron microscope view of a *D. uniflora* seed bearing an elaiosome and noted that in this species the elaiosome is globose or irregularly elongated, "reaching 0.5 to 2.5 times as long as the seed." Elaiosomes are shown on the seeds in Fig. 1C.

Berg (1969) considered this species to be myrmecochorous and speculated that the "lustrous black" seed coat, as well as the elaiosome, were both attractive to ants. Berg illustrated a fruit apparently chewed open by ants, and described two small field experiments from 1964 where *D. uniflora* seeds set out in "depots" (small piles of 10 fresh seeds) were carried away in a few minutes by ants (*Formica lasioides* in El Dorado County, and *F. fusca* in Alpine County, CA). In the field, we have only very rarely observed ants taking elaiosomes from *D. uniflora* fruits, but suspect that ant dispersal is at least an occasional part of the life history of this species in Butte County. Berg (1969) discussed in detail the probable evolution of myrmechochory in *Dicentra*. He suggested that *D. uniflora*, showing a "minimum number of diaspores produced at ground level" probably represents a unique pathway ("blind end") in evolution of ant dispersal in the genus, as compared with taller myrmechohorous species like *D. formosa*.

Seed germination. Stern (1961) noted that seeds of *Dicentra* need three months of stratification before germination; he may have been referring to *D. formosa* and not *D. uniflora*. No earlier information is available on the germination of *D. uniflora* seeds. Some of the features we describe are similar to those described for other geophytes: germination in the soil during the winter, fast production of underground parts that remain dormant over the summer, and a short life above ground before dying down to a dormant below ground organ (Dafni et al. 1981). These life cycle features are known to occur in several other geophytic species that occur with *D. uniflora* at all three main study sites, such as *Triteleia ixioides* (W. T. Aiton) Greene subsp. *anilina* (Greene) L. W. Lenz, (Kannely and Schlising 2014), *Allium campanulatum*, and *Sanicula tuberosa* (Schlising, unpublished data).

It is particularly noteworthy that the tiny *Dicentra* seedlings have the only several weeks to establish a below ground organ that will initiate growth the next year, formed by photosynthesis (and possibly by transferring nutrients from the endosperm in the seeds) and growing a structure above the root that has been called a "bulblet" by Stern (1961), or referred to as a "bulbous leaf base" by Walton and Hufford (1994). These small white structures (Fig. 1D) on the seedlings are only about 10% of the size of bulblets that are found on on mature (flowering) individuals (Fig. 1F).

Finding an apparently single cotyledon in this dicot was surprising (Fig. 1D). However, the phenomenon of "pseudomoncotyly" (or "monocotyledony") in the dicots is briefly described in older textbooks of plant morphology (e. g., Eames 1961) and is reprised more recently based on experimental studies of embryo morphogenesis (Titova 2000). However, mention of the single cotyledon specifically for *Dicentra* is very rare in the literature, [e.g., "1 in tuberous *Corydalis* and a few *Dicentra* species" (Lidén 1993)].

Herbivory on Whole Plants or Reproductive Parts

It is likely that the "missing" fruits described under "Fate of Flowers in 2018" relates in part to having been grazed by black-tailed deer. Percentages of developing fruits probably lost to deer may be high: Ridge S: 29%; Meadow: 25%; and Summit: 30% in 2018 (Fig. 6), and in all years of this study missing fruits—often with the pedicel still present—were noted at each main study site. Rayl (2002) reported that rodents ate a few of the non-bagged flowers/fruits in her study but provided no information on which species of rodents. She also reported 18% (in 2000) and 16 % (in 2001) of her non-bagged flowers/fruits were lost to predation. These percentages are slightly smaller than those seen in our study in 2018 (Fig. 6). Cameras in the field would help ascertain loss to deer. Rick Whittsell (Chico State University, personal communication), who has studied the black-tailed deer in Butte County, confirms that they are able to select small parts of plants with their tongues. Thus, in the early spring (when *Dicentra* fruits are forming) they could be a nutritious food source when there are still few sources of fresh plant growth available. Is it also possible, that *D. uniflora* has achieved some of its wide geographic range via dispersal of seeds in feces of deer. Myers et al. (2004) reported that seeds from 70 plant species, including native herbs, were germinated from fecal pellets of white-tailed deer (*Odocoileus virginianus* Zimm.) in New York State. They concluded that white-tailed deer represented a significant and previously unappreciated vector of seed dispersal. One unknown aspect concerning herbivory is whether the alkaloids common in species of *Dicentra* are toxic to deer, as this species has been reported to cause occasional livestock poisoning in cattle (Stern 1961).

The mature fruits that we collected for seed counts were not totally desiccated and dry, and Berg (1969) even considered fruits to be "greenish and somewhat fleshy at maturity, and made of living chlorenchyma and not desiccated tissues." Thus, the discovery of the caterpillar of *Parnassius clodius* on an apparently masticated fruit (still attached to the plant but lying on the ground) suggests that this species could potentially be responsible for some destruction. Scott (1986), Pyle (2002), and James and Nunnallee (2011) describe the butterfly as having *D. uniflora, D. pauciflora* and *D. formosa* as host plants on which the larvae feed in spite of poisonous alkaloids in the plant tissues (Scott 1986). All three species of *Dicentra* occur at Meadow and Summit study sites. Adult butterflies lay over-wintering eggs, often in the litter on the ground in the vicinity of *Dicentra* plants (Pyle 2002; James and Nunnallee 2011). The several instars of the larvae apparently consume *Dicentra* leaves and possibly green fruit tissue during the short, several-week above ground growth period of the plant. Furthermore, the larvae feed nocturnally (Pyle 2002). This may explain why we did not observe any larva earlier in the study, although we have not noted insect damage on the leaves either. The larva collected was a late instar of *P. clodius* (Fig. 1G).

Leaf Base Tubers (Bulblets)

Function of the leaf base tubers (bulblets) produced on flowering *D. uniflora* plants, as well as on its seedlings, can be partially understood based on the work of Walton and Hufford (1994). These authors published detailed work on the below ground structures in the closely related *D. cucullaria*, which flowers early in the spring in deciduous forests in the northeastern U.S. and adjacent Canada; they included brief comments on *D. uniflora*. The underground bulblets of *D. uniflora,* like those that we have measured and have also planted, are presently referred to as bulblets in several floras (e.g., Stern 1961; Baldwin et al. 2012), and we have used that term in this study. Bulblets in *Dicentra* are leaf base tubers, each with the potential for producing a new plant from a minute, undeveloped bud at its base, if the leaf base tuber is detached from the parent plant as stated by Walton and Hufford (1994). Walton and Hufford (1994) noted that these bulbous leaf bases in the four related species of *Dicentra* (*D. cucullaria, D. canadensis* Walp., *D. pauciflora*, and *D. uniflora*) are unique in the angiosperms.

Walton and Hufford (1994) also suggested that stored carbohydrates in "amyloplast-filled storage parenchyma cells" in these leaf base tubers (bulblets) of *D. cucullaria* may be utilized in forming above-ground organs by this plant during its short growing season. Photosynthesis occurring at that time provisions new leaf base tubers (bulblets). Walton and Hufford (1994) describe continued belowground development during the summer months for *D. cucullaria.*

However, unlike *D. cucullaria*, *D. uniflora* has a large, fleshy root-like tuber, in addition to bulblets. The shrinking of the old tuber in *D. uniflora* probably provides carbohydrates to the emerging flowering plant, and the production of a new tuber is, at least in part, provisioned by photosynthesis. Once *D. uniflora* plants senesce, no further growth would be expected in the belowground tubers and bulblets during the dry, hot summer months in Butte County.

The production of a bulblet by a *D. uniflora* seedling (Fig.1D)—very quickly before summer drought sets in—is the only way a seedling can survive to a second year. Usually a *D. uniflora* plant in its second spring bears a brownish, shrunken (depleted) bulblet, a new whitish bulblet, and also a small tuber (Fig. 1E). Harper (1977) pointed out that it is not unusual for geophytes to have a long juvenile phase and require four to seven years or longer to reach flowering age. It is not known how many years it takes before an individual flower is produced in *D. uniflora* (Mackey, unpublished data).

Potential Historical Change in Phenology

The study areas at Carpenter Ridge are at the lower elevation of *D. uniflora* in Butte County. Areas here are aligned along a Crescent (Fig. 1A) with exposure from southwest to north, with area N warmer and area S colder than the other areas evaluated at this site. Therefore, snowmelt is earlier at N than at S. Meadow and Summit are at intermediate elevations over the range of elevations of *D. uniflora* in California. Analysis of trends in snowpack across California have indicated reduced snowpack at intermediate and lower elevations in more recent years (Howat and Tulaczyk 2005; He et al. 2015). There is also an apparent increase of slightly less than one degree C from 1970 to 2017 in statewide annual average temperatures, and a shift of almost a month earlier in average peak runoff in the Sacramento River system from mid-April to mid-March (OEHHA 2018). A better understanding of the life history responses and growth of *D. uniflora* to snow cover, snowmelt, and dry and wet seasons could potentially provide information on the long-term climate change in northern California.

Our ongoing use of field plantings of seeds and bulblets and our continued long-term evaluation of flowering and underground features will provide a better understanding of the timing and growth patterns of this ephemeral geophyte.

ACKNOWLEDGEMENTS

Help in the field was provided by Robert Fischer, Tim Hanson, and Samantha Hillaire. Research in Lassen Volcanic National Park was conducted under permit LAVO-2010-SCI-0001.

We thank Colleen Hatfield and Lawrence Janeway, of the Chico State Herbarium, for use of herbarium equipment, without which this study would not have been possible. We are grateful to Gail Vanderhoof, Design Graphics at Chico State University, for producing the colored plate, and to Mariby Cruz, Chico State University, for statistical analysis. We appreciate the many helpful comments and suggestions by reviewers.

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Appendix 1

Voucher specimens for *Dicentra uniflora* are filed at California State University, Chico (CHSC). Butte County, CA, close to Tehama County line, on Carpenter Ridge, southwest of Butte Meadows, 2 mi E of junction with Highway 70 (T25N, R3E, NW ¼ of NW ¼ Section 1), elevation 4350 feet; volcanic mudflow outcrop within conifer forest; 27 April 2009; *R. A. Schlising 4471 and H. E. Mackey, Jr.* Butte County, CA, close to Tehama County line, on Carpenter Ridge, southwest of Butte Meadows, 2 mi E of junction with Highway 70 (T25N, R3E, NW ¼ of NW ¼ Section 1), elevation 4350 feet; volcanic mudflow outcrop within conifer forest; 13 May 2009; *R. A. Schlising 4472 and H. E. Mackey, Jr.* Butte County, CA, E of Jonesville, near NE tip of the county, ca. 0.75 mi S of Humbug Summit, on Humbug Summit Road; margin of forest of *Abies magnifica*; in conifer litter; 28 June 2017; *R. A. Schlising 4678 and H. E. Mackey, Jr.* Butte County, CA, 6.6 km east of Jonesville, and 0.32 km south of the road leading up Scotts John Creek, on U.S. Forest Service road 26N27, at 40°06′21.0″ latitude N, 121°25′35.40″ longitude W, and at 1746 m elevation; in open, drying meadow between dense forest of mainly *Abies concolor* and meadow remaining wet all summer; 6 June 2018; *R. A. Schlising 4679 and H. E. Mackey, Jr.*